ARDISIA CRENATA Sims

Ardisia crenulata Lodd. Bot. Cab. **1**: *pl. 2.* 1817. *Nomen nudum,* based on cultivated specimens from China.

Ardisia crenata Sims, Curtis's Bot. Mag. **45**: *pl. 1950.* 1818. Proposed as a new name for *A. crenulata* and accompanied by a description.

Ardisia lentiginosa J. B. Ker, Bot. Reg. **7**: *pl. 533.* 1821. Proposed as a change of the name *A. crenata* Sims, because of *A. crenata* Roxb. Hort. Beng. 85. 1814. That name, however, was a *nomen nudum* until the publication of a description in Roxb. Fl. Ind. ed. Carey **2**: 276. 1824. This name appears frequently in Japanese literature.

Ardisia crispa (Thunb.) A. DC., as misapplied in Trans. Linn. Soc. London **17**: 124. 1834; DC. Prodr. **8**: 134. 1844. DeCandolle transferred *Bladhia crispa* Thunb. but described *A. crenata* Sims, which he placed as a synonym.

An erect shrub or undershrub up to 1.5 m high, the glabrous stem usually unbranched except for the special flowering branches; leaves chartaceous or coriaceous, elliptic-lanceolate or oblanceolate, acute or acuminate, 6 to 20 cm long, 2 to 4 cm wide, generally crisped or undulate, with large albuminous marginal glands, glabrous, usually raised-punctate at least beneath, very sparingly lepidote below, the lateral nerves 12 to 18 pairs, uniting into a generally distinct marginal nerve, this sometimes hidden beneath the recurved edge; inflorescences simple or compound, subumbellate or cymose, terminal on special lateral or axillary branches about 10 cm long, these sometimes up to 16 cm long or longer, bearing a few leaves generally only at or near the curved apex, but sometimes scattered, glabrous; flowers white or pink, 4 to 6 mm long, the sepals 1.5 mm long, oblong-ovate, rounded or obtuse, scattered-punctate, the anthers distinctly punctate on back; fruit 5 to 8 mm in diameter, punctate.

Japan to southern continental Asia.

PALEOBOTANY.—*Some American fossil plants belonging to the Isoetales.*[1] ROLAND W. BROWN, U. S. Geological Survey.

In 1889 Lester F. Ward[2] described at length but did not name some sunflowerlike rosettes from two localities in the Fort Union formation (early Tertiary) along the Yellowstone River, respectively 12 miles above and 28 miles below Glendive, Mont. In *The synopsis of the flora of the Laramie group* published in 1886, he had already alluded to these fossils as "singular cryptogams." Not, however, until 1915, in *Glimpses of the Cosmos,* a posthumous volume, did he name them *Xantholithes propheticus.*

The general superficial appearance of the more perfect of these specimens is that of a flower having numerous long, narrow rays attached to a small circular center, the whole sometimes attaining a diameter of 30 cm. The rays are 2 to 3 mm in width for most of

[1] Published by permission of the Director, Geological Survey, Department of the Interior. Received March 1, 1939.

[2] WARD, LESTER F. *Remarks on an undescribed vegetable organism from the Fort Union group of Montana.* Amer. Assoc. Adv. Sci. Proc. **37**: 199–201. 1889.

their length but terminate in a spatulate, blunt-pointed expansion. The particular feature that immediately arouses special interest is the presence of two parallel, closely-spaced rows of squarish cavities or protuberances, depending on the specimen, through the middle of the spatulate expansion and for some distance in the remainder of the ray. Ward reported these squarish outlines as being arranged in pairs; but examination of numerous specimens shows that alternations are not rare. The spatulate end of the ray has a smooth, lateral flange, which, along the narrower portion toward the base of the ray, becomes an undulate ribbon or ruffle. Because portions of the rock matrix remained in the depressions of the undulations of this ruffle when the specimen was uncovered, the ruffle appears broken, and Ward supposed that the margin of the ray was toothed. In the specimens seen by Ward the margin is entire; but a Cretaceous species I collected just east of the ghost town of Cumberland, Wyo., during the field season of 1938, has a serrate margin around the spatulate end of the ray. In regard to the surface pattern, Ward reported that "examination with a high power reveals the presence of a continuous epidermal membrane composed of hexagonal cells." Fig. 4 shows the surface pattern magnified 13 times, but the cells are square to rectangular, not hexagonal.

In order to determine the affinities of this organism Ward sought the opinion of many eminent paleontologists, botanists, and zoologists, with no very definite results, some even suggesting the possibility that the fossils might represent an animal, not a plant. The latter supposition is not altogether fantastic when viewed in the light of remarkable coincidences or resemblances. Thus, in 1900 John M. Clarke[3] described a marine organism from the Devonian of western New York as *Paropsonema cryptophya*, a supposed echinoderm. Clarke's figures are, however, not so suggestive as they might be if they illustrated U. S. National Museum specimen 62948 taken from the Ithaca member of the Portage group (Upper Devonian) in the excavation for the library at Cornell University. This almost perfect specimen is so much like the rosettes here being discussed that, did the specimens not occur in totally different environments and at widely separated moments of geologic time, they might, on hasty or superficial examination, well be confused.

Ward, however, himself concluded:

I am disposed to regard it as a "comprehensive type" of vascular crypto-

[3] CLARKE, JOHN M. *Paropsonema cryptophya, a peculiar echinoderm from the intumescens zone (Portage beds) of western New York.* New York State Mus. Bull. **39**: 172–186, pls. 5–9. 1900.

gamic life, embodying some of the characters of several well-known living types, viz., 1. The large tufted central base is suggestive of most species of *Isoetes*, and the long weak stems [rays] of certain of these species are observed to recline and lie prostrate in all directions around this center. 2. The double row of spore-cases [median cavities] at the apex of the stem [ray] agrees in all essential respects with that of *Ophioglossum*, and the elliptic expansions may be regarded as homologues of the larger blade-like fronds of that genus, which may easily be imagined to have the spores borne along its median line instead of on a special fruiting frond. 3. The prostrate sinuous habit is not widely unlike that of certain creeping species of *Lycopodium* . . . . 4. A still further approach is seen in *Selaginella* where the scales have become distichous and the stems flat and closely creeping . . . . 5. Finally, ignoring the appendicular organs of *Marsilia*, we see in the fruit-bearing portion a further analogy to our fossil, the fruiting stems [rays] radiating from the thickened base and bearing the spores at their apex. The fossil would thus represent a highly generalized type and may be phylogenetically related to all these more specialized modern forms with each of which it seems to possess some characters in common.

In his reply dated August 2, 1888, to Ward's request for suggestions as to the affinities of this organism, Leo Lesquereux made two penetrating observations. First, the organism looked like that described by J. W. Dawson in 1883 as *Carpolithes horridus*. Second, the long slender "branches" are "peculiar organs of floating plants." Coming close to the latter idea also was the reply by W. G. Farlow, dated July 31, 1888, who inquired, "Have you considered the possibility of it being a whorl of inflated leaves like those of the upper portions of some Utriculariae?"

Dawson conjectured that his specimen, described and figured in 1883 as from Cretaceous strata on the Peace River in northeastern British Columbia, was a "compound fruit perhaps of some cycadaceous plant, covered with bracts and rudimentary leaves." The figure, if faithfully drawn, represents an imperfect specimen, showing none of the spatulate ends of the rays. In 1886 Dawson renamed his original specimen *Antholithes horridus* and reported additional fragmentary material from Cretaceous strata [Kootanie series, according to Dawson] on Old Man River, southwestern Alberta. He reiterated their reference to the Cycadaceae.

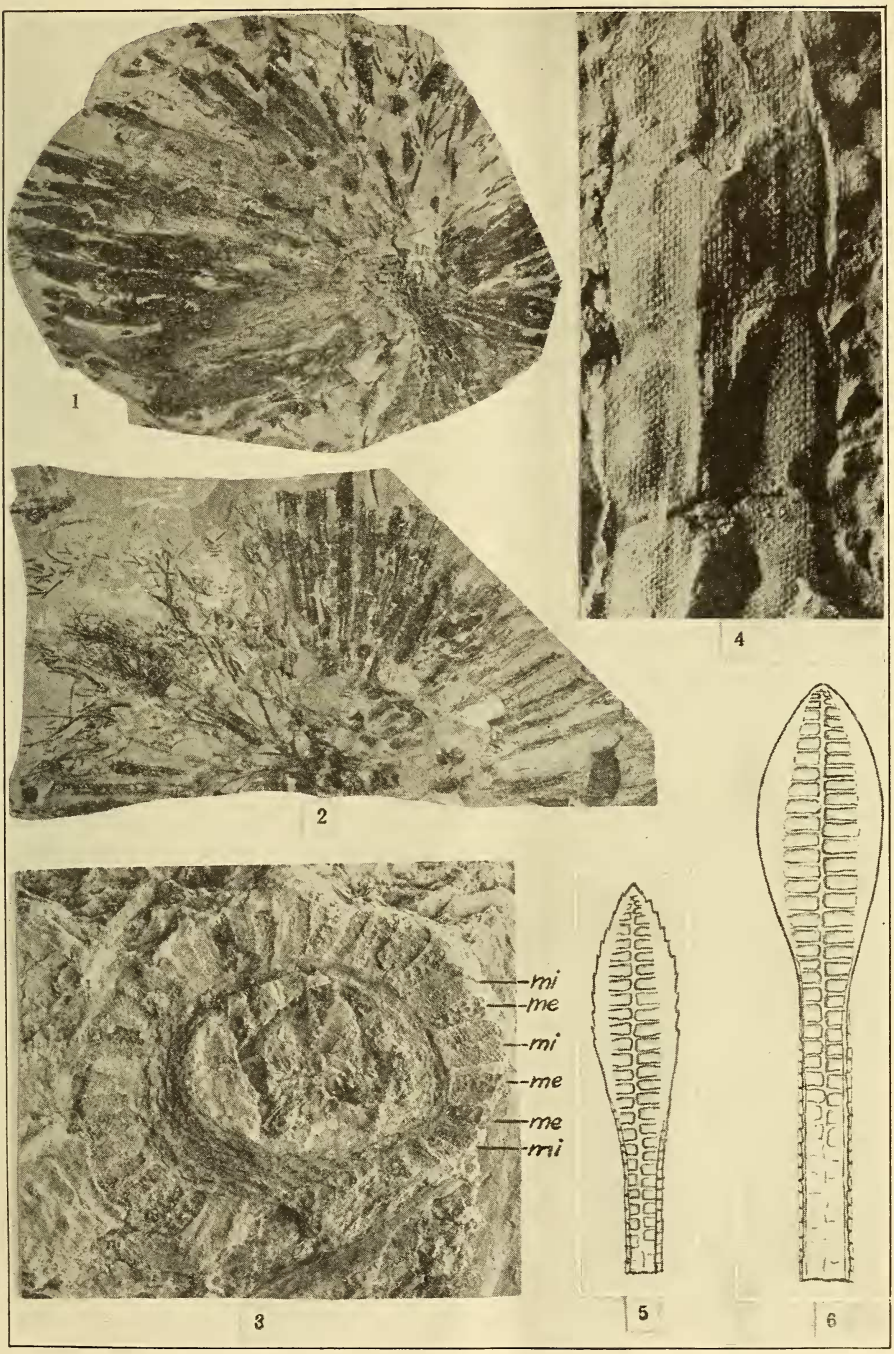
Ward never published an illustration of *Xantholithes propheticus;* but this lack was met by Knowlton in 1923, Cockerell in 1924, and Berry in 1935 (see synonymy of *Isoetites horridus* for references). Knowlton was concerned with a specimen from the Green River formation (middle Eocene) in Colorado, which he confidently referred to *Danaea*. That specimen is a fragment; consequently, when Cockerell in 1924 described a better specimen from the Wind River Basin of Wyoming as an *Ophioglossum*, Knowlton began to have doubts

about his specimen being a *Danaea*, and agreed with Berry, who in the meantime had received additional material from Wyoming, that none of these specimens were *Ophioglossum* but were probably related to Ward's *Xantholithes propheticus* from the Fort Union formation. However, in a letter dated December 15, 1924, Knowlton remarked to Berry that, because his fragment of *Danaea* lacked the prominent flange displayed by the terminal portions of Ward's *Xantholithes propheticus*, it was likely that his *Danaea* was after all a different thing. In 1930 Berry reviewed the whole matter, calling all the Wyoming and Colorado material simply "sporophylls" and suggesting that these organisms "might represent a relict form of some member of the Williamsoniales." In 1934 I also reviewed the situation insofar as it concerned the *Danaea* specimen from the Green River formation and suggested that it be considered tentatively as distinct. With most of the specimens referred to in the discussion up to this point before me and with new collections made during the past few years of field work in Montana, Wyoming, and Colorado, I am now of the opinion that all these organisms are congeneric and represent species belonging to the Isoetales. The basis for this opinion will be apparent after considering the evidence derived from a reexamination of some features of the specimens and bringing all information about these organisms up to date.

The epidermal pattern of rectangular cells covers the entire surface of the rays uniformly; that is, it may be observed not only on the smooth surface but in the median depressions and protuberances of the "spore cases" and the undulations of the marginal ruffles as well (Fig. 4). If the median squarish outlines were indeed spore cases, these areas should display a somewhat broken or heterogeneous surface; but this is not the case; the surface is a homogeneous pattern throughout. I conclude, therefore, that these rays were leaves with crispate or wavy membranous margins in the basal portions and with midsections that carried a double row of undulations that may have been sharp wrinkles or the external outlines of internal air sacs, which, on fossilization, collapsed, leaving a series of squarish cavities.

Figs. 1, 2, 4, 5.—*Isoetites serratus* Brown, n. sp. Figs. 1 and 2 show dichotomous roots beneath the rosettes of leaves. Fig. 4 shows the surface pattern of a leaf, ×13. Fig. 5 is the spatulate end of a leaf showing the serrate margin, the ruffled, membranous, lower margin and the parallel rows of median squarish depressions, ×2. From the Frontier formation (Upper Cretaceous), 1 mile east of Cumberland, Wyo.

Figs. 3, 6.—*Isoetites horridus* (Dawson) Brown, n. comb. Fig. 3 shows a section of the corm, a set of spirally arranged leaf scars, and a circle of sporangia, *mi* (microsporangia), *me* (megasporangia), at the bases of an outer whorl of leaves, ×3. From the Fort Union formation (early Tertiary) on Poison Spider Creek, 35 miles west of Casper, Wyo. Fig. 6 is the spatulate end of a leaf showing the entire margin, ×2. From the Fort Union formation on the Yellowstone River at Burns Ranch, Mont.



Figs. 1–6.—(See opposite page for description.)

It should be noted that the outside margins of these median undulations are not so sharp as those on the inside but generally fade imperceptibly into the broad marginal flange. There is no trace of venation in these leaves, except for a thickened median line that may have been a structure analogous to a midrib. Transverse to this "midrib," especially in the proximad portion of the leaf, are scattered bars that may have been internal septa.

The plant with its radial arrangement of leaves constituted either a floating rosette or one that was close to the soil or mud in a well-watered situation. In the specimens (Figs. 1, 2) from the base of the Frontier formation in Wyoming I found immediately beneath the rosette a radiating system of dichotomous, filiform organs that appear to have been roots. The leaves of the rosette were attached spirally to a very much shortened, thick, upper portion of a stem or corm. This is clearly shown in a specimen (Fig. 3) which I collected in 1936, together with much material of the separate, broken leaves, from the Fort Union formation on Poison Spider Creek, 35 miles west of Casper, Wyo. At Burns Ranch, Mont., *Xantholithes propheticus* is associated on the same slabs of rock with *Trapa? microphylla* Lesquereux, a hydrophyte with a floating rosette and submerged, fimbriate, filiform leaves, anchored by a threadlike stem or root.[4]

Finally, the specimen (Fig. 3) from Poison Spider Creek also fortunately preserves the clue to the identity of all these specimens. At the bases of the leaves are elliptic bodies of two kinds, one filled with large cavities (*me*) that were once occupied by rounded objects having ridges and a variety of surface sculpture, the other filled with cavities (*mi*) only one-third or one-fourth the size of the former and once filled with rounded objects that appear to have been comparatively smooth. The comparison of these elliptic bodies and their contents with the sporangia and the megaspores and microspores of *Isoetes* is obvious and is strengthened when the entire anatomy of the fossils and their habit are compared with those of *Isoetes*.

The interested reader will find a detailed discussion of the quillworts, *Isoetes*, in Pfeiffer[5] and Clute.[6] It will be sufficient for the present purpose to cite only the facts that may apply to the specimens under discussion.

Isoetes is essentially a rosette of numerous, short, rushlike, pointed

[4] Brown, Roland W., and Houldsworth, Edgar. *The fruit of Trapa? microphylla Lesquereux.* This Journal 29: 36–39, figs. 1–9. 1939.

[5] Pfeiffer, Norma. *Monograph of the Isoetaceae.* Ann. Missouri Bot. Gard. 9: 79–232. 1922.

[6] Clute, Willard N. *The fern allies.* New York 1905.

leaves, with sporangia in their axils, attached spirally to a very compact 2- or 3-lobed corm from the hollows of which arise many dichotomously branched roots. A single collateral bundle runs through the center of the leaf, and this, together with some surrounding tissue, separates the hollow interior into four parallel chambers having many cross partitions. Proximad the leaves have membranous margins, and on the inner face near the base they carry a little flap of tissue called a ligule. The surface pattern is a homogeneous fabric of rectangular cells. Only the outer, earlier whorls of leaves produce sporangia, the outermost producing megaspores, the inner, microspores. Both are produced on the same plant, but in some species at different seasons. The megaspores can be seen with the naked eye, but they are generally 10 to 20 times larger than the microspores. The megaspores are white, divided equatorially by a ridge into two hemispheres, one of which is no farther divided, but the other is divided by ridges into three nearly equal triangular areas. The surface is variously patterned with spines, tubercles, pits, and serpentine forms, affording important features for specific identification. The microspores are somewhat irregularly oblong and have a smooth or slightly roughish surface. There are about 50 species of *Isoetes*, with representatives in most parts of the world, but in general each species is remarkably restricted. So far as habitat is concerned, they are classed as submerged, amphibious, and terrestrial.

By comparison with the data just given, the fossils differ from all living species of *Isoetes* in the following particulars: (1) The megaspores are only 3 or 4 times the size of the microspores, unless the objects here called microspores are immature megaspores. (2) The leaves terminate in spatulate ends, with or without serrate margins. (3) As the specimens showing sporangia are fragmentary at the point where ligules should be looked for, nothing is definite as to the presence or absence of a ligule. (4) The outline of the cross section of the corm, although somewhat irregular, shows no lobing.

Fossils most similar to the American specimens have been described by Saporta[7] from the Lower Cretaceous of Portugal as *Isoetes choffati*, now called *Isoetites choffati* (Saporta) Seward.[8] Reviewing the fossil Isoetaceae, Seward remarked that "if Saporta's . . . species . . . is correctly determined, it is the oldest fossil member of the family and indeed the most satisfactory among the more than doubtful species

[7] SAPORTA, LE MARQUIS DE. *Flore fossile du Portugal.* Direct. Trav. Geol. Portugal, p. 134, pl. 24, fig. 2b, 9–11; pl. 25, figs. 5–8; pl. 27, fig. 6, 1894.

[8] SEWARD, A. C. *Fossil plants* 2: 66–68. 1910.

described as extinct species of *Isoetes*. . . . Such evidence as we have lends support to the inclusion of these Portuguese fossils in the genus *Isoetes*, but apart from the fact that we have no proof of any connexion between the stems and supposed sporophylls, the resemblance of the latter to those of *Isoetes* is, perhaps, hardly sufficient to satisfy all reasonable scepticism. . . . ." It is hoped that the skepticism, avowed by Seward in regard to Saporta's Portuguese specimens, may now be removed by the evidence supplied from the American specimens reported here. As regards Saporta's *Isoetopsis subaphylla* from the Eocene of Aix-en-Provence, continued doubt as to its relationship with the Isoetaceae must be entertained.

Although not founded upon very satisfactory material, the genus *Isoetites* Münster seems to have precedence and to be most appropriate for the fossils here under consideration. I distinguish two American species: *Isoetites serratus* Brown, with spatulate leaf ends having serrate margins, and *Isoetites horridus* (Dawson) Brown, with spatulate leaf ends having entire margins.

To E. W. Berry and W. R. Maxon I am grateful for specimens and an exchange of ideas concerning these fossils.

All specimens figured here are in the U. S. National Museum.

Isoetites serratus Brown, n. sp. Figs. 1, 2, 4, 5

Rosettes of narrow, strap-shaped leaves with spatulate ends having a serrate margin. The margin of the narrow portion of the leaves is entire, membranous, and ruffled. The median line of the leaves is marked by two parallel, closely spaced rows of squarish cavities or protuberances, depending on the specimen. Immediately beneath the rosette of leaves is a radiating system of dichotomously branched roots. The leaves and roots are attached to a rounded, compact corm.

This species differs from *Isoetites horridus* (Dawson) Brown chiefly in having a serrate margin around the spatulate ends of the leaves. Whether some other Cretaceous specimens now synonymized with *I. horridus* should be included with *I. serratus* is a question that can be decided only when better-preserved material from those localities is found.

Occurrence.—Base of the Frontier formation (Upper Cretaceous), in shales weathering white, exposed in a bluff on the south side of Little Muddy Creek, 1 mile east of Cumberland, Wyo. (Figs. 1, 2, 4, 5).

Isoetites horridus (Dawson) Brown, n. comb. Figs. 3, 6

Carpolithes horridus Dawson, Roy. Soc. Canada Trans. 1 (sec. 4): 21, pl. 1, figs. 3, 3a, 36. 1883.

Antholithes horridus (Dawson) Dawson, idem. 3 (sec. 4): 7. 1886.

Vegetable organism, Ward, Amer. Assoc. Adv. Sci. Proc. 37: 199–201 1889.— Idem, 6th Ann. Rept. U. S. Geol. Surv.: 534, 544. 1886.

Xantholithes propheticus Ward, *Glimpses of the Cosmos*, p. 150. 1915.—Berry, Geol. Surv. Canada Mem. **182**: 65, pl. 20. 1935.
Williamsonia marylandica Berry, *Upper Cretaceous*, Maryland Geol. Survey, p. 769, p. 51, figs. 5, 6. 1916.
Danaea coloradensis Knowlton, U. S. Geol. Surv. Prof. Paper **131**: 150, pl. 36, fig. 4. 1923.—Berry, Torreya **24**: 49. 1924.—Brown, U. S. Geol. Surv. Prof. Paper **185–C**: 52. 1934.
Ophioglossum hastatiforme Cockerell, Torreya **24**: 10, with text fig. 1924.
Xantholithes hastatiformis Cockerell, Torreya **26**: 10. 1926.
Sporophylls, Berry, U. S. Geol. Surv. Prof. Paper **165**: 78. 1930.

This species is morphologically similar to *Isoetites serratus* Brown, except that it appears to be represented by larger specimens and has entire margins around the spatulate ends of the leaves. The specimens from Poison Spider Creek, Wyo., in addition show sporangia in the axils of the leaves, the only American examples so far reported. These are similar to *Isoetites choffati* (Saporta) Seward from Portugal, but as the latter species is not represented by specimens showing the character of the leaf ends, it is not possible to make further comparisons between it and the American species.

It may be that I have included in the synonymy some names attached to fragmentary material which when better material from the same localities or formations is found may necessitate some reallocations. In the meantime the books will be cleared of a number of names now given to several incomplete specimens.

Occurrence.—In Cretaceous (according to Dawson), on forks of Pine River and Peace River, British Columbia; Kootanie series (according to Dawson), on middle branch of north fork of Old Man River, southwestern Alberta; Mentor formation (Lower Cretaceous), 8 miles south of Hanston, Hodgeman County, Kans.; Magothy formation (Upper Cretaceous), Little Round Bay, Anne Arundel County, Md.; Tullock formation (early Tertiary), on Moon Creek, 10 miles west of Miles City, Mont.; in carbonaceous shales (early Tertiary) in North Dakota, 3 miles north of Watauga, South Dakota; Fort Union formation (early Tertiary), on Poison Spider Creek, 35 miles west of Casper, Wyo. (Fig. 3); idem, west flank of Cedar Creek anticline, 12 miles southwest of Glendive, Mont.; idem, left bank of Yellowstone River at Burns Ranch, 28 miles northeast of Glendive, Mont. (Fig. 6); Ravenscrag formation (early Tertiary), northwest sec. 35, T. 5, R. 1 W. of 3d meridian, Saskatchewan; probably Wasatch formation (Eocene), southwest $\frac{1}{4}$ sec. 18, T. 6 N., R. 4 W., north of Tipperary, Wyo.; Green River formation (middle Eocene), Rio Blanco County, Colo.